



REPLY TO BEST AND ASHBY:

The concept of evolutionarily stable strategies (ESS) helps link ecology and evolution

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To demonstrate the existence of an evolutionarily stable strategy (ESS) in fluctuating ecological systems (such as predator–prey system with limit cycles) is important. Deriving the analytic conditions for such an ESS can be of great help when studying real biological systems. A main aim of our study (1) was just that. Rather than saying “extended the ESS concept to be applicable for periodically fluctuating ecological systems,” we should have said (cf. ref. 2) “further extended the applicability of the ESS concept to periodically fluctuating ecological systems.” Specifically, we have generalized the Reed and Stenseth (3) ecologically based ESS approach to a periodically fluctuating ecological system.

We do agree, however, that we have a good foundation [including, of course, the papers referred to by Best and Ashby (2)] for future work aiming at integrating

ecology and evolution. Unfortunately, evolutionary questions are too often addressed within ecologically stable systems. Similarly, ecological questions are too often addressed without simultaneously considering evolutionary changes. Our study (including those we cited)—as well as those cited by Best and Ashby—is important in our effort to understand how ecological and evolutionary processes interact. As pointed out by Sigmund and Holt (4), we “may be at the threshold of a fully fused theoretical understanding of coupled ecological and evolutionary dynamics, deepening our understanding of organic diversity and pertinent to many urgent applied problems” (p. 2). Our generalization (1) of the ecologically based ESS approach published by Reed and Stenseth (3) may provide a good platform for linking the ecological and the evolutionary processes.

- 1 K. Grunert, H. Holden, E. R. Jakobsen, N. C. Stenseth, Evolutionarily stable strategies in stable and periodically fluctuating populations: The Rosenzweig–MacArthur predator–prey model. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2017463118 (2021).
- 2 A. Best, B. Ashby, Evolutionarily stable strategies are well studied in periodically fluctuating populations. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.2102001118 (2021).
- 3 J. Reed, N. C. Stenseth, On evolutionarily stable strategies. *J. Theor. Biol.* **108**, 491–508 (1984).
- 4 K. Sigmund, R. D. Holt, Toward ecoevolutionary dynamics. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2100200118 (2021).

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